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Description of the immature stages and bionomics of *Anthonomus* (*Anthonomus*) *brunnipennis* Curtis, 1840 (Coleoptera, Curculionidae, Anthonomini)

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Abstract

The developmental stages (larva, pupa) of *Anthonomus brunnipennis* are fully described for the first time. Despite great similarities of the adults of *A. brunnipennis* and *A. rubi* the differences between immature stages of both species could be demonstrated. Two different habitats of *A. brunnipennis* in Germany are described, and host plant data are critically reviewed. The only well-documented host plant of *A. brunnipennis* is *Potentilla erecta*.

Key Words

Anthonomini, *Anthonomus brunnipennis*, biology, Curculionoidea, larva, morphology, *Potentilla erecta*, pupa

Introduction

With more than 500 species, the genus *Anthonomus* Germar, 1817 (Curculioninae, Curculioninae) is the largest genus in the tribe Anthonomini (Clark 2005, 2013; Caldara 2013). Approximately 400 of them occur in the Neotropics, 73 in the Palaearctic, 3 in the Afrotropics, 11 in the Oriental Region, and 2 in the Australian and Pacific Regions (Clark 2005, 2013; Caldara 2013; Sprick and Floren 2018). They are characterized by small to medium-sized bodies (1.7–5.0 mm), elongate rostra, long antennae, somewhat convex eyes, small pro-femorae and teeth on the pro- and mesofemorae (Smreczyński 1972; Burke 1976). *Anthonomus* weevils are known to inhabit 22 different plant families (Dieckmann 1968; Anderson 1993; Jones 2001). The majority of them feed on dicotyledonous plants, the larvae develop in flower buds, and pupation takes place in flower buds or rarely in soil (Koch 1992). Certain larvae, like those of *A. phyllocola* (Herbst, 1795), develop in conifer flowers. A small number of larvae are known to develop as inquilines of galls (e.g., *Anthonomus vis* Clark, 1992 on *Leandra aurea* Cogn. (Melastomataceae) produced by momphid moth larvae (Lepidoptera, Momphidae) (Gates and Burke 1972).

Knowledge about the morphology of immature Anthonomini stages is restricted to around 10% of the species, but compared with other speciose genera or tribes, it is at a quite good but still nowhere near sufficient level, as descriptions from some subgenera are non-existent (Zabaluev 2021). Burke (1968) published descriptions and illustrations of the pupae of 47 species, which were later supplemented by descriptions of the larvae of several dozen Anthonomini species by Ahmad and Burke (1972) and Burke and Gates (1974). The latest comprehensive contribution with first descriptions of some Palaearctic species – *Anthonomus* (*Anthonomidius*) *rubripes* Gyllenhal, 1835, *A.* (s. str.) *incurvus* (Panzer, 1795), *A.* (s. str.) *conspersus* Desbrochers des Loges, 1868, and *A.* (s. str.) *latior* Pic, 1902 – was provided by Zabaluev (2021). Other studies give information on the biology and morphology of immatures of the Nearctic

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species *A. monostigma* Champion, 1903 (Chacón-Madrigal et al. 2012), *A. rubricosus* Boheman, 1859 (Loiácono et al. 2004), *A. vis* (Bená and Vanin 2013) and *A. santacruzi* Hustache, 1924 (Gosik et al. 2017).

Although certain species, such as *Anthonomus rubi* (Herbst, 1795), *A. pomorum* (Linnaeus, 1758), *A. vestitus* Boheman, 1859 and *A. grandis* Boheman, 1843, have been identified as significant pests (Scherf 1964; Burke 1976), and conversely, *A. santacruzi*, *A. morticinus* Clark, 1998 and *A. monostigma* are employed as biocontrol agents of weeds (Burke 1976; Olckers 1999; Caxambu 2003; Chacón-Madrigal et al. 2012), knowledge of the biology of many other Anthonomini species is rudimentary. According to Zabaluev (2021), the bionomics of fewer than 12% of Palaearctic *Anthonomus* species have been studied to date.

Anthonomus brunnipennis is a European species with a range limited to several countries in the western and northern part of the continent, namely, Belgium, Denmark, Great Britain, Northern Germany, France, Ireland and Switzerland; in Scandinavia and north-eastern Europe it occurs in Finland, Norway and Sweden, also in Latvia, Lithuania and the northern part of European Russia (Alonso–Zarazaga et al. 2023). According to Hoffmann (1954), Dieckmann (1968), Palm (1992) and Morris (2012), *Comarum palustre* L., *Dryas octopetala* L., *Filipendula ulmaria* (L.) Maxim. and *Potentilla erecta* (L.) Raeusch. (all Rosaceae) are mentioned as host plants of *A. brunnipennis*.

Our aim is to describe the morphology of the immature stages, larva and pupa of *Anthonomus brunnipennis*, with particular emphasis on the differences between this species and its sibling species *A. rubi*, and to update and expand knowledge about the bionomics of *A. brunnipennis*.

In addition, based on the available descriptions of larvae, in particular by Ahmad and Burke (1972), Burke and Gates (1974), Zabaluev (2021), the differences between genera of the tribe Anthonomini have been formulated.

Materials and methods

Insect collection

Larvae: 9 exx. of various instars: collected on 15.06.2022: 3 exx. breeding to 23.06.2022; 1 ex. breeding to 23.06.2022; 4 exx. breeding to 17.06.2022; 1 ex. breeding to 05.07.2022.

Pupae: 4 exx. collected on 15.06.2022, 1 ex. breeding to 05.07.2022.

All specimens collected in Germany, National Park Harz, mountain meadow, in part wet, from *Potentilla erecta* (L.) Raeusch.

In order to confirm species affiliation, some of the larvae obtained in the field were left to metamorphose under laboratory conditions (Fig. 1A, B). The adults were determined based on the morphological features proposed by Palm (1992).

Morphological descriptions

All larval and pupal specimens described were fixed in 95% ethanol and examined under an optical stereomicroscope (Olympus SZ 60 and SZ11) with calibrated oculars. The following measurements of larval instars were made: body length (BL), body width (BW) (at the second abdominal segment) and width of the head capsule (HW). The body length (BL) of pupae was measured without urogomphi.

Slide preparation basically followed May (1994). Larvae selected for study under a microscope were dissected, cleared in potassium hydroxide (KOH, 10%), then rinsed in distilled water. After clearing, the head and mouthparts were separated and mounted on permanent microscope slides in Faure–Berlese fluid (50 g gum arabic and 45 g chloral hydrate dissolved in 80 g of distilled water and 60 cm^3 of glycerol) (Hille Ris Lambers 1950).

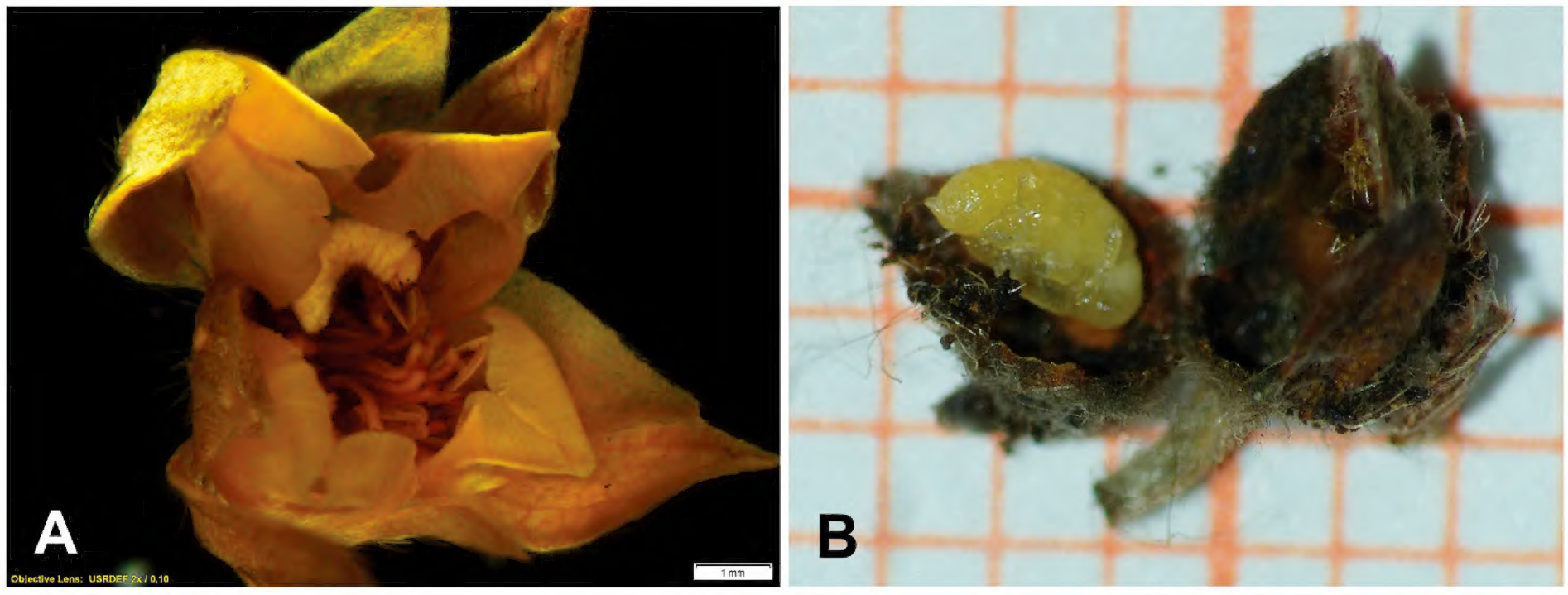


Figure 1. Breeding of *Anthonomus brunnipennis*. **A.** Young larva in a flower bud of *Potentilla erecta*; **B.** Pupa in a flower bud of *Potentilla erecta* after the 11th day of breeding.

Photographs were taken using an Olympus BX63 microscope and processed with Olympus cellSens Dimension software. The larvae selected for SEM imaging (scanning electron microscope) were first dried in absolute ethanol (99.8%), then rinsed in acetone, treated by CPD (Critical Point Drying) and finally gold–plated. TESCAN Vega 3 SEM was used to examine selected structures. The general terminology and chaetotaxy follow Anderson (1947), May (1994), Marvaldi (1997, 1998, 1999, 2003) and Skuhrovec et al. (2015), while the antennae terminology follows Zacharuk (1985). In the case of the description of the pupa, we followed the terminology proposed by Skuhrovec et al. (2015).

Morphological abbreviations

Abd. I–X–abdominal segments 1–10, **Th. I–III**–thoracic segments 1–3, **at**–antenna, **clss**–clypeal sensorium, **ds**–digitiform sensillum, **st**–stemmata, **Se**–sensorium, **sa**–sensillum ampullaceum, **sb**–sensillum basiconicum, **snp**–sensilla pores, **tra**–terminal receptive area, **lr**–labral rods, **ur**–urogomphus; setae: ***als***–anterolateral, ***ams***–anteromedial, ***as***–apical (pupa), ***cls***–clypeal, ***d***–dorsal (pupal abdomen), ***des***–dorsal (larval head), ***dms***–dorsal malar, ***ds***–discal (pupal prothorax), ***ds***–dorsal (larval abdomen), ***eps***–epipleural, ***eus***–eusternal, ***fs***–frontal, ***les***–lateral epicranial, ***ligs***–ligular, ***lrs***–labral, ***ls***–lateral, ***lsts***–laterosternal, ***mbs***–malar basiventral, ***mds***–mandibular, ***mes***–median, ***mps***–maxillary palp, ***pda***–pedal, ***pds***–postdorsal, ***pls***–posterolateral, ***pes***–postepicranial, ***pfs***–palpiferal, ***pms***–postlabial, ***prms***–prelabial, ***prns***–pronotal, ***prs***–prodorsal, ***ps***–pleural, ***sls***–superlateral, ***sos***–superorbital, ***ss***–spiracular, ***stps***–stipal, ***ves***–ventral, ***vms***–ventral malar, ***vs***–vertical. **HW**–head width, **BL**–body length, **BW**–body width.

Results

Habitat and host plant

The habitat (Fig. 2A–C) in the National Park Harz near Drei Annen Hohne, Sachsen-Anhalt (Fig. 2A, B, E), is a nutrient and base-poor wet meadow on a slightly inclined slope of the types Junco acutiflori-Molinietum and Crepido-Juncetum acutiflori (see Preising et al. 1997) with plants such as *Crepis paludosa* (L.) Moench, *Deschampsia cespitosa* (L.) P. Beauv., *Filipendula ulmaria*, *Galium uliginosum* L., *Hypericum maculatum* Crantz, *Juncus acutiflorus* Ehrh. ex Hoffm., *Plantago lanceolata* L., *Potentilla erecta* (host plant of *A. brunnipennis*), *Ranunculus acris* L., *Rubus idaeus* (host plant of *A. rubi*), *Senecio ovatus* (Gaertn. et al.) Willd., *Succisa pratensis* Moench, *Valeriana dioica* L., *Valeriana excelsa* Poir. s. str. and many others.

The habitat of *Anthonomus brunnipennis* in the Hechtmoor in Mittelangeln, northern Schleswig-Holstein (Fig. 2C, D, F) is part of a peat bog. At the *A. brunnipennis* site it contains plant species such as *Calluna vulgaris* (L.) Hull, *Comarum palustre* (syn. *Potentilla palustris*), *Erica tetralix* L., *Eriophorum angustifolium* Honck., *Lysimachia vulgaris* L., *Molinia caerulea* (L.) Moench, *Potentilla erecta* (host plant), *Sphagnum* spec., and *Vaccinium oxycoccos* L. Due to a lack of a complete plant recording the plant community is not exactly known, it could belong to Sphagno-Juncetum acutiflori or Carici-Agrostietum caninae, which unites the presence of all, or most, recorded plant species (see Preising et al. 2012).

This plant community, more characterized by peat bog rather than wet meadow conditions, may describe another extreme of the plant communities, in which *P. erecta* and *A. brunnipennis* can be found in Germany.

Morphology

Description of the mature larva of *A. brunnipennis*

BL: 2.46–2.66 mm; BW: 0.70–0.83 mm; HW: 0.53–0.56 mm.

General habitus (Fig. 3A, B). Colour of living larva and pupa yellowish; head capsule always light brown.

Body strongly curved, rounded in cross section. Prothorax prominent, pronotal shield weakly isolated, not more sclerotized than rest of prothorax; meso- and metathorax almost equal in size. Meso- and metathorax each divided dorsally into two folds (prodorsal folds small, postdorsal folds prominent). Pedal lobes of thoracic segments weakly isolated and flattened. Abdominal segments I–V of a similar, medium size, with next segments tapering towards posterior body end. Abdominal segments I–VII, each with three dorsal folds, prodorsal and postdorsal folds well developed, the later divided into two parts (the first narrow, the second slightly wider and much higher than the first). The divisions and subdivisions are most visible on abdominal segments I-V and become gradually faint from abdominal segment VI onwards. Segment VIII with a wide prodorsal fold and a narrow, undivided postdorsal fold. Abdominal segment IX undivided dorsally. Epipleural, laterosternal and eusternal folds of segments I–VIII slightly conical and weakly isolated. Abdominal segment X divided into four folds of almost equal size, completely hidden within segment nine. Anus situated ventrally. All spiracles bicameral: thoracic ones (Fig. 3C) placed medio-laterally on the prothorax, abdominal ones (Fig. 3D) placed medio-laterally on segments I–VIII. Body cuticle densely covered with nodular asperities and only partially smooth (Fig. 4A–D).

Chaetotaxy (the number of setae is given for one side of the body) (Fig. 4A–D). Setae of various lengths, from elongate to minute, always hair-like. Thorax (Fig. 4A): prothorax with 9 elongate and 1 short *prns* (6 on the pronotal sclerite, the next 3 above the spiracle), 2 elongate

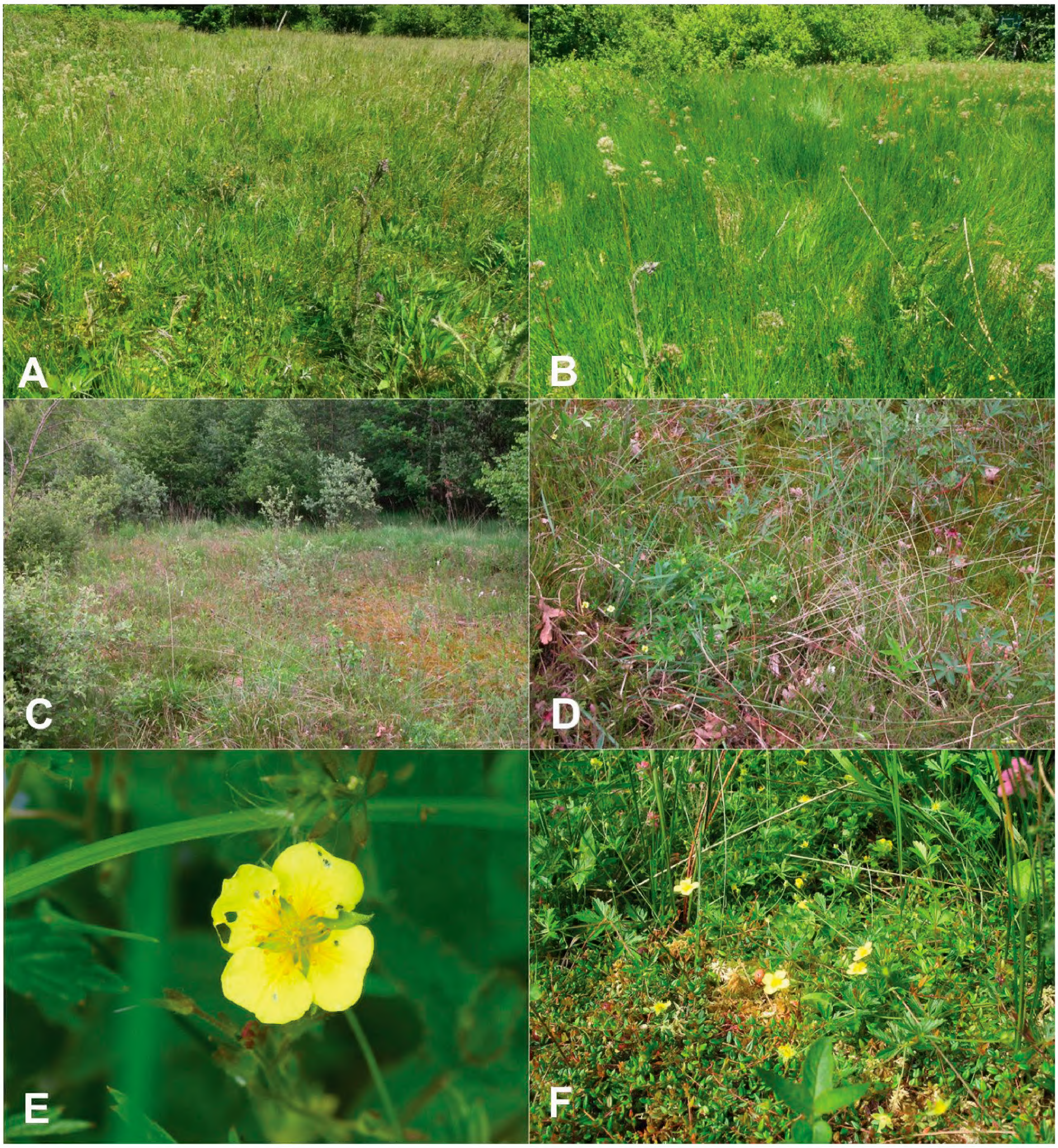


Figure 2. Habitat of *Anthonomus brunnipennis* in the Harz Mountains and in Schleswig-Holstein. **A.** Wet meadow of the type Junco-Molinietum with *Potentilla erecta* in the National Park Harz near Drei Annen Hohne; **B.** Wet meadow with large stands of *Juncus acutiflorus* in the Harz Mountains, in direct contact to the habitat depicted on A; **C.** Habitat of *A. brunnipennis* in the Hechtmoor in Schleswig-Holstein; **D.** Habitat in the Hechtmoor with *Comarum palustre* and *Potentilla erecta*. **E.** *Potentilla erecta* in the habitat of *A. brunnipennis* in the Harz Mts. with feeding holes. **F.** Detail from the habitat in the Hechtmoor with *Potentilla erecta* and *Vaccinium oxycoccos*.

ps, and a single elongate *eus*. Meso- and metathorax each with 1 minute and 1 medium *prs*, 4 *pds* of various lengths (first long, second medium, third and fourth long), spiracular area with 2 *ss* of various lengths (1 long and 1 minute), 1 long *eps*, and 1 long *ps*. Pedal areas of thoracic segments, each with two elongate and one medium *pda*. Abdomen (Fig. 4B, C): segments I–VIII with 1 minute and 1 medium *prs*, 4 *pds* (first and third elongate, second and fourth medium), 2 *ss* (first minute, second medium), 2 *eps* (1 medium and 1 minute), 1 minute *lsts*, and a single minute (sometimes absent) *eus*. Abdominal segment IX with 3 very long *ds* and 2 *ps* (1 long, 1 minute). Segment X: anal lobes without setae (Fig. 4D).

Head (Figs 5A–C, 6A, B, 7A, B). Head capsule almost rounded; endocarinal line long, two-thirds as long as frons; frontal sutures distinct along entire length up to

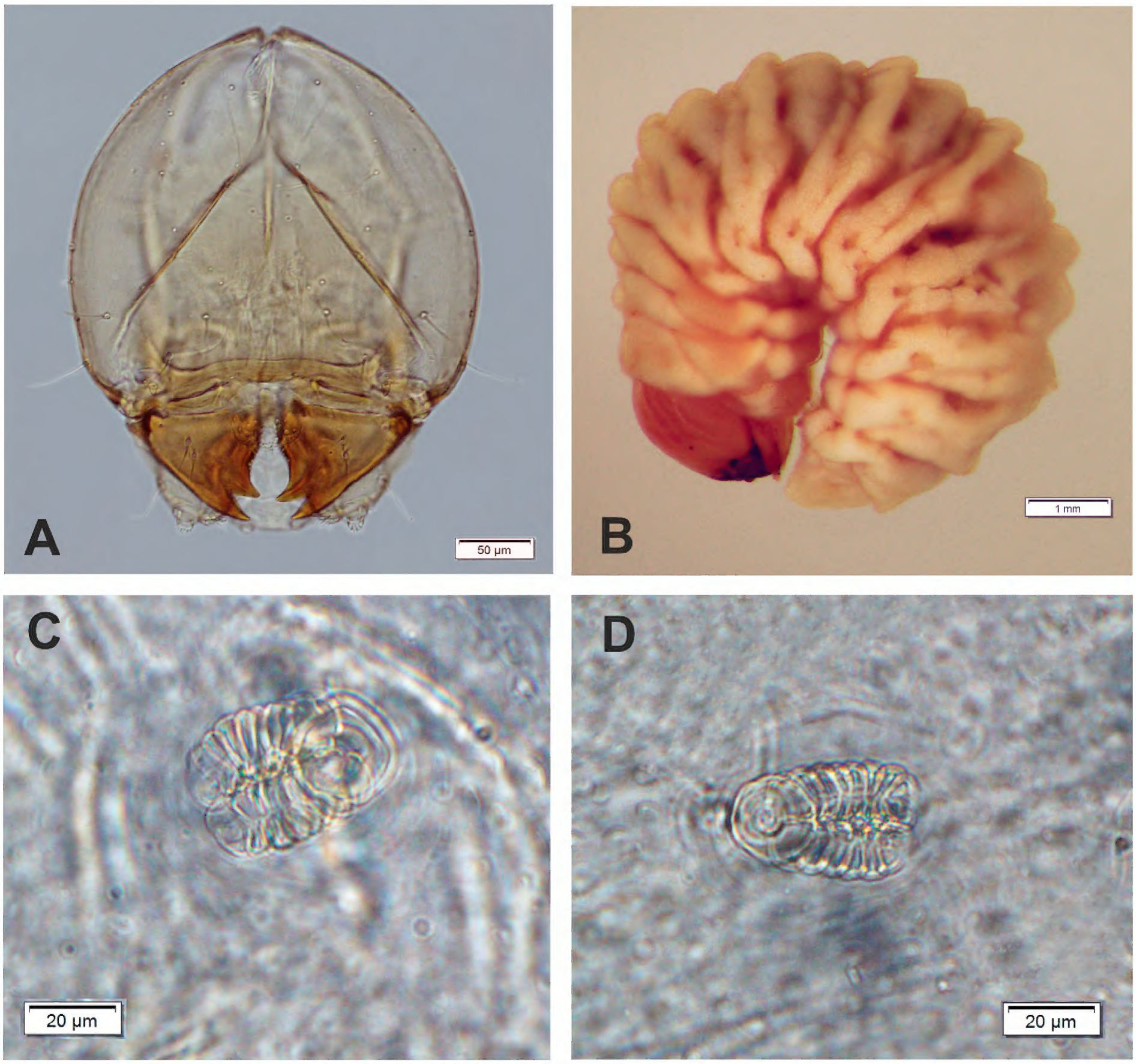


Figure 3. *Anthonomus brunnipennis*. **A.** Head; **B.** Larva, habitus, lateral view; **C.** Spiracle of prothorax; **D.** Spiracle of abdominal segment I.

antennae; one single stemma present on each side (st) in form of prominent dark pigmented spots with convex cornea, placed anterolaterally (Fig. 5A). Each hemisphere of head with 16 setae of various lengths, from medium to minute. Cranial setae: des_1 medium, placed medially, des_2 medium, placed posterolaterally, des_3 medium size, placed on epicranium close to frontal suture, des_4 short, placed anteromedially, des_5 medium, placed anterolaterally, fs_1 minute, placed posteriorly, fs_3 minute, placed anteromedially, fs_4 medium, placed anteromedially and fs_5 medium, placed close to epistome, les_1 short, les_2 as long as des_5, two *ves*: first minute, second medium, postepicranial area with 3 minute *pes*.

Antennae (Fig. 6A, B) with frontal position on each side at anterior margin of head; membranous basal segment convex, semi–spherical, bearing conical, elongate sensorium and 6 sensilla: 5 basiconica (sb) and 1 ampullaceum (sa).

Mouthparts (Figs 7A–E, 8, 9A, B, 10A–D). Clypeus (Fig. 7A, B) approximately 3× wider than long, cls_{1-2} short, placed posterolaterally. Anterior margin of clypeus almost straight. Labrum (Fig. 7A, C, D) trapezium-shaped, approximately 2.3× wider than long; lrs_1 long, placed medially, lrs_2 long, placed antero-laterally and lrs_3 short, placed antero-laterally. Epipharynx (Fig. 7E) with 3 digitate *als*, equal in length, 3 *ams*, various in size and shape: ams_1 elongate, rod-like, ams_2 thin, ams_3 very short and curved; mes_1 short, mes_2 robust, curved. Labral rods (lr) elongate, more sclerotized at apex, distinctly converging posteriorly. Sensilla pores (snp) arranged in a single median cluster of 4 units, close to *ams*.. Surface of epipharynx between labral rods smooth. Mandibles (Fig. 8) with 2 apical teeth of unequal height, the inner one apical and very robust. Cutting edge between apex and middle of mandible smooth. Both setae, mds_1 and mds_2, medium, placed medially in shallow depressions.

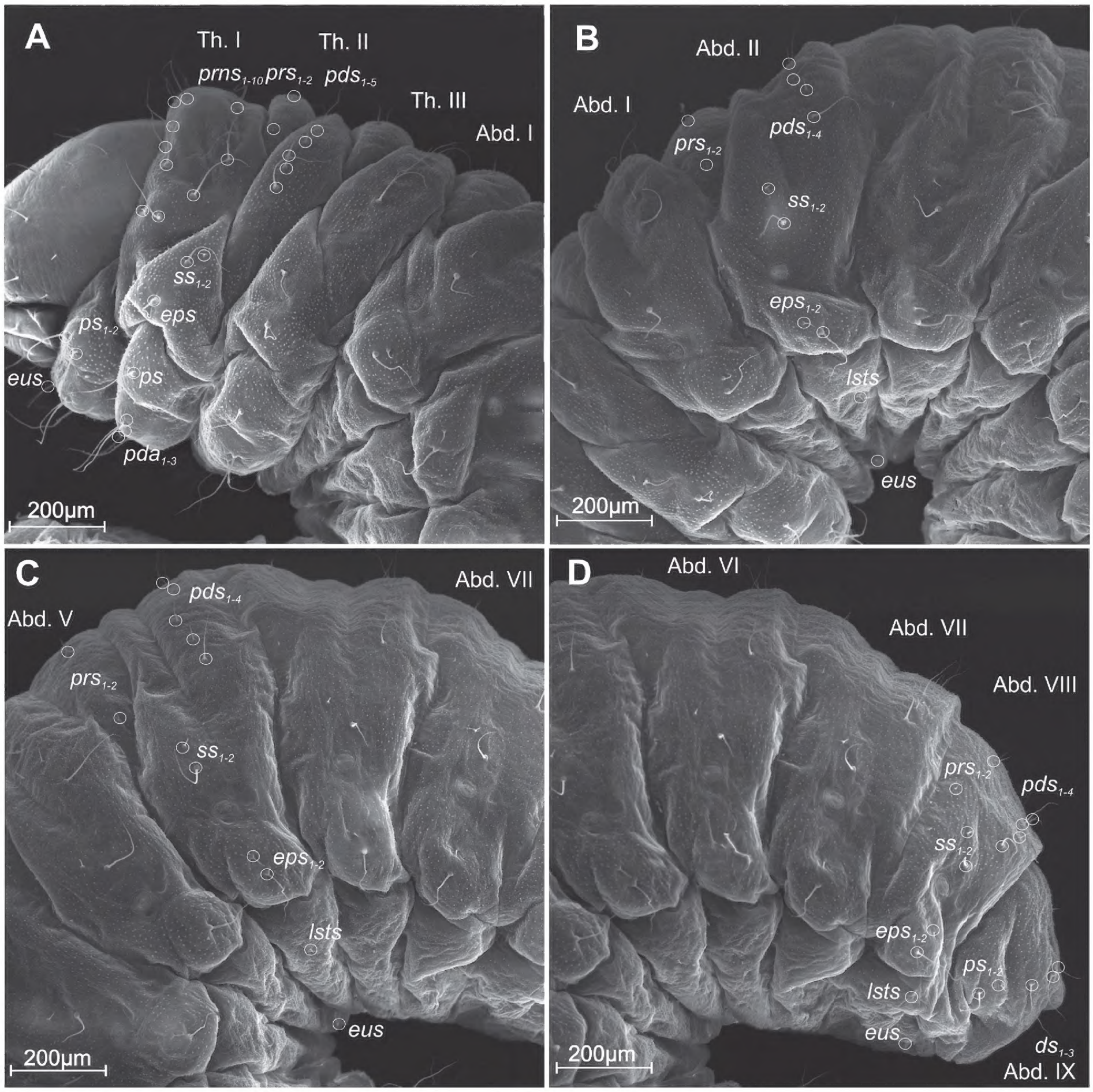


Figure 4. *Anthonomus brunnipennis* mature larva, habitus and chaetotaxy, lateral view (SEM micrographs). **A.** Head and thorax; **B.** Abdominal segments I–III; **C.** Abdominal segments IV–VII; **D.** Abdominal segments VI–IX (setae: *ds*–dorsal, *ps*–pleural, *eps*–epipleural, *eus*–eusternal, *lsts*–laterosternal, *pda*–pedal, *pds*–postdorsal, *prns*–pronotal, *prs*–prodorsal, *ss*–spiracular).

Maxillolabial complex (Figs 7B, 9A–C, 10A–D) on stipes with 1 elongate *stps* and 2 medium size *pfs*. Mala with a row of 6 digitate, almost equally sized *dms* and 4 rod-like *vms* (2 medium and 2 short). Maxillary palps with two palpomeres; basal palpomere distinctly wider than distal one. Length ratio of basal to distal palpomeres almost 1:1. Basal palpomere with medium *mps* and 2 pores, distal palpomere (Fig. 9A–C) with 1 pore, 1 digitiform sensillum (ds) and a group of 10 apical sensilla (8 basiconica and 2 ampullacea) on terminal receptive area (tra) (Fig. 10A–D). Dorsal parts of mala smooth. Labium with prementum cup–shaped, with 1 medium *prms* placed medially. Ligula concave, semicircular at margin, with 3 *ligs* (one short, two minute). Premental sclerite trident–shaped (median branch weakly sclerotized), posterior extension with elongate, sharp apex; postmentum moderately narrow, membranous, triangular, divided by two furrows into three parts of different size; 3 *pms*, various in size: pms_1 medium, located medially, pms_2 elongate, mediolaterally and pms_3 short, placed anterolaterally. Labial palps two–segmented; basal palpomere wider and much shorter than distal one. Length ratio of basal to distal palpomeres almost 0.5:1. Basal palpomere with two pores, distal with a single pore and a group of 9 apical sensilla (basiconica) on a terminal receptive area. Posterior and posterolateral parts of labium covered with prominent, nodular asperities (Fig. 9A).

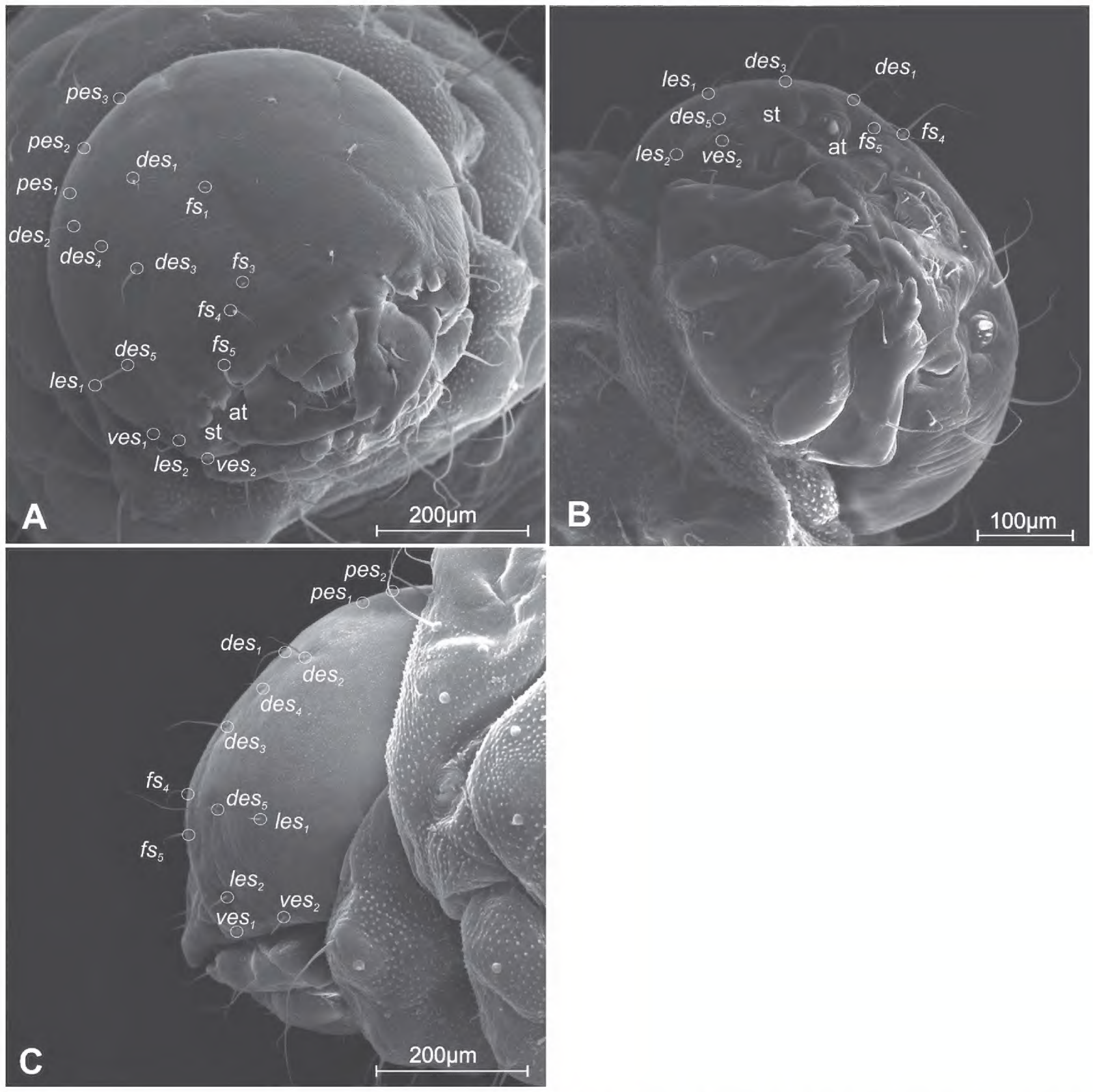


Figure 5. *Anthonomus brunnipennis* larva, head. **A.** Mature instar, frontal view; **B.** Mature instar, ventral view; **C.** Mature instar, lateral view, scheme (at–antenna, st–stemmata, setae: *des*–dorsal epicranial, *fs*–frontal, *ls*–lateral epicranial, *pes*–postepicranial, *ves*–ventroepicranial).

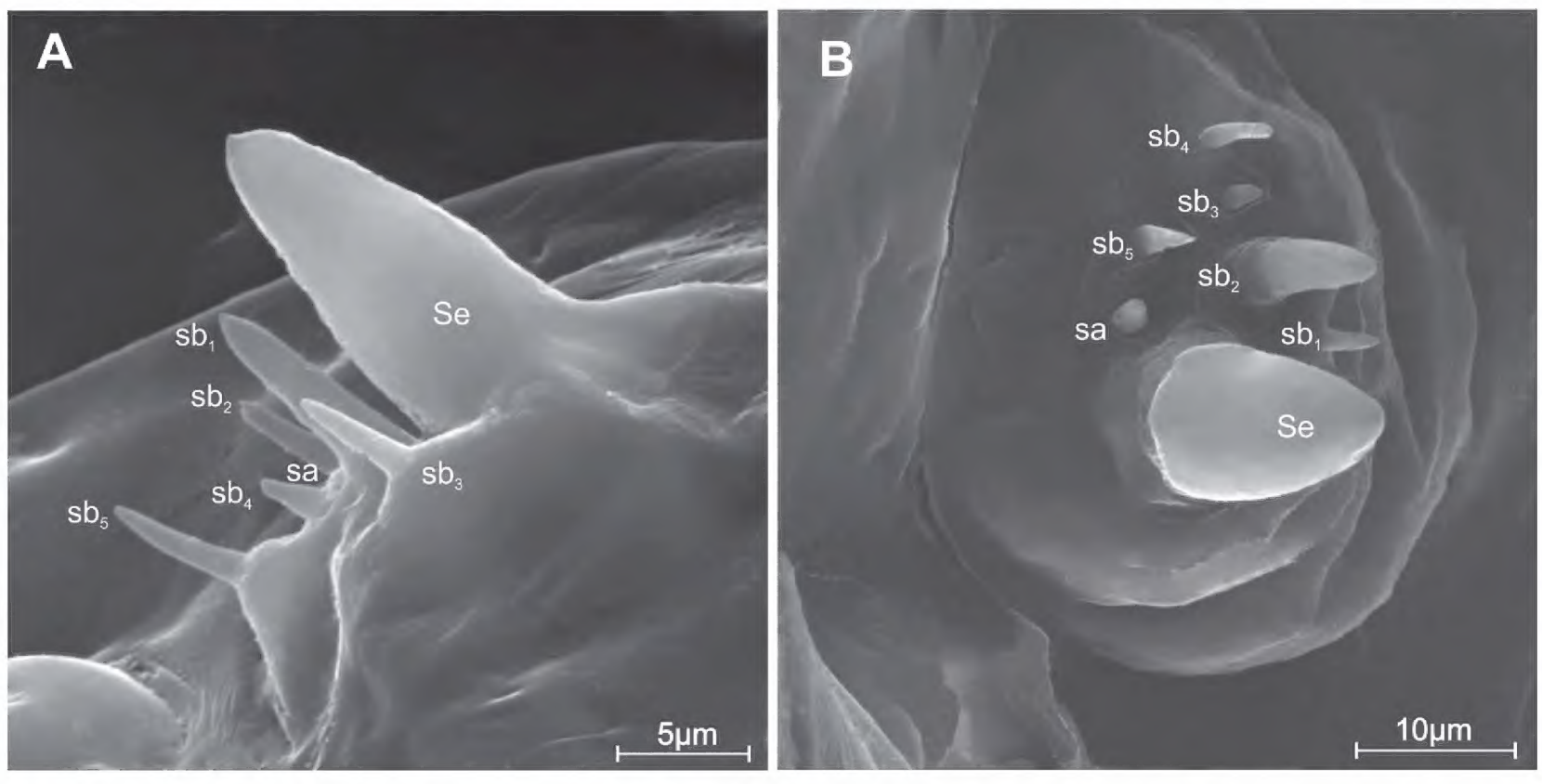


Figure 6. *Anthonomus brunnipennis* mature larva, antenna (SEM micrograph). **A.** Lateral view; **B.** Dorsal view (sa–sensillum ampullaceum, Se–sensorium, sb–sensillum basiconicum).

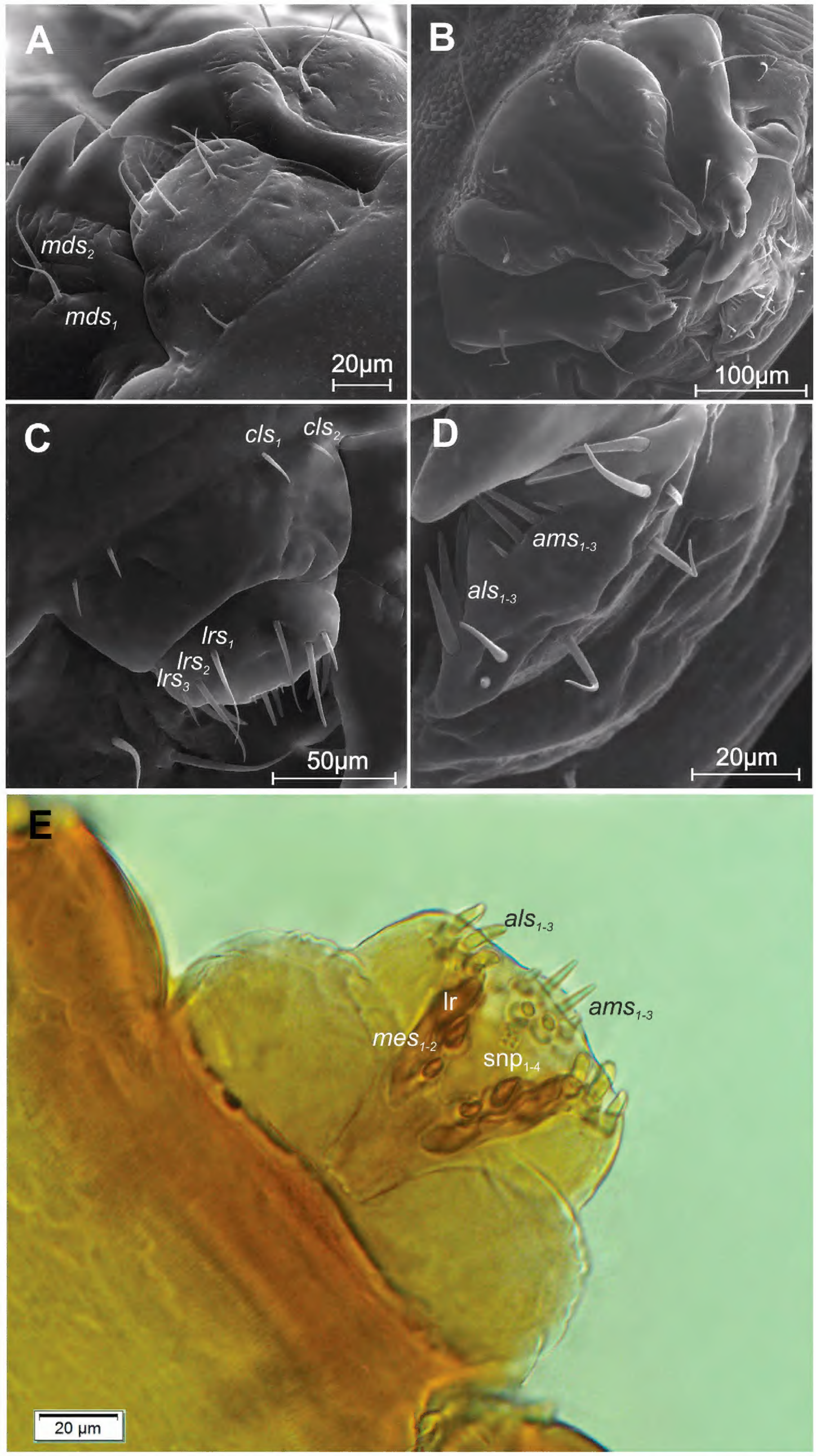


Figure 7. *Anthonomus brunnipennis* mature larva, mouthparts. **A.** Total, dorsal view (SEM micrograph); **B.** Total, ventral view, (SEM micrograph); **C.** Clypeus and labrum, dorsal view, (SEM micrograph); **C.** Clypeus and labrum, dorsal view (SEM micrograph); **D.** Labrum, frontal view, (SEM micrograph); **E.** Epipharynx, (photo) (lr–labral rods, snp–sensilla pores, setae: *als*–anterolateral, *mds*–mandibular, *ams*–anteromedial, *cls*–clypeal, *lrs*–labral, *mes*–median).

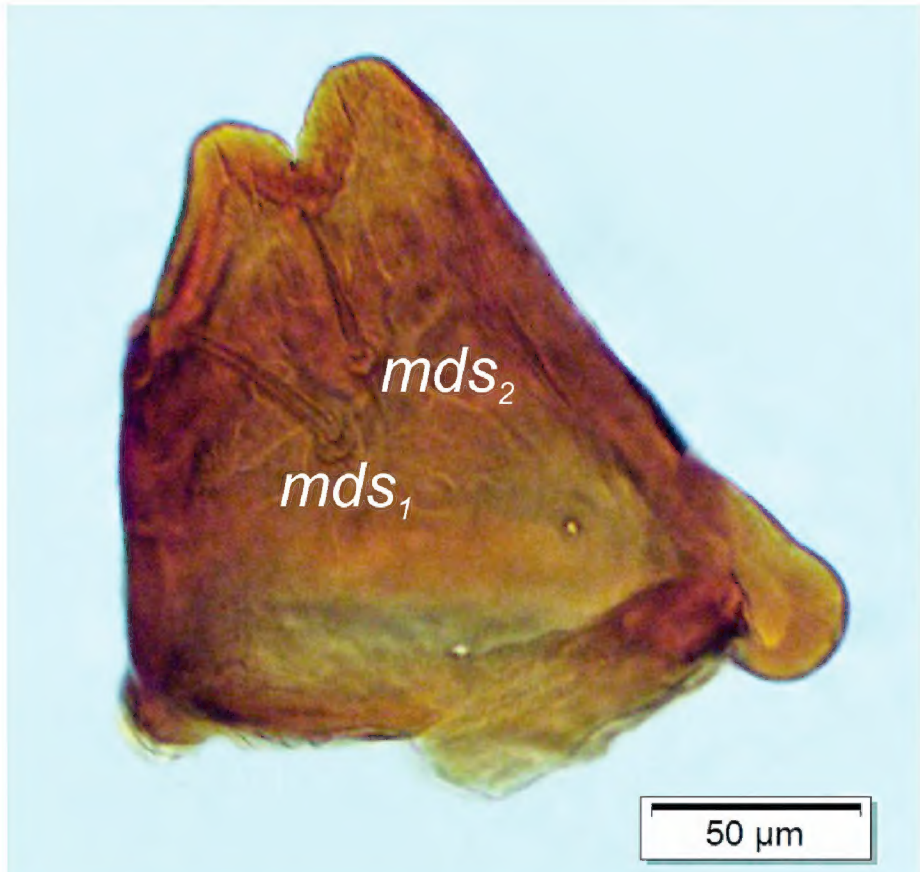


Figure 8. *Anthonomus brunnipennis* mature larva, right mandible, (photo) (*mds*–mandibular seta).

Description of the pupa of *Anthonomus brunnipennis*

General habitus and chaetotaxy (Figs 11, 12A, B). Body yellowish, 1.90–2.30 mm in length, stout, cuticle partially covered with fine, nodular asperities (Fig. 12D). Rostrum very elongate, 6× as long as wide, almost reaching gonothecae. Pronotum 2.5× wider than long, trapezium-shaped. Prothoracic depression present. Mesonotum narrower than metanotum. Abdominal segments I–V of equal length, segments VI and VII tapering gradually towards end of body, segment VIII narrow, segment IX terminal, with urogomphi (ur) medially situated, straight, rather short, fused. Only the apical parts of urogomphi free, apices curving to the outside. Surface of urogomphi covered with asperities. Male gonothecae undivided, female gonothecae divided, with tubercles on subcontiguous lobes (Fig. 13C, D). Spiracles placed dorso–laterally on abdominal segments I–VI, functional on segments I–V, vestigial on segment VI.

Chaetotaxy (setal numbers given for one side of the body): setae variable in size, hair–like, placed on conical or thorn-like protuberances. Head with short, 1 *vs* and 2 *sos* short, rostrum with 1 *rs* minute. All setae on head and rostrum placed on small, conical protuberances (Fig. 12C, D). Pronotum with 1 *as*, 2 *sls*, 2 *ds* and 3 *pls* almost equal in size. Ds_1 placed on robust, thorn-like protuberance, ds_2 and pls_{1-3} placed on medium-sized, thorn-like protuberances; $ls_{1,2}$ placed on small, conical protuberances. Meso– and metathorax with 3 setae, various in length, placed medially on dorsum. Abdominal segments I–VII with 5 setae, various in length (seg. VII without d_4) even setae are visibly shorter than the odd ones, d_{1-3} located along posterior margin of the segment, d_4, placed antero-laterally and d_5 medio-laterally. Setae: $d_{1,2,4}$ placed on small conical protuberances, $d_{3,5}$ placed on thorn-like protuberances. Segment VIII with 2 elongate setae, placed on robust, thorn-like protuberances (Fig. 13B). Segment IX without setae. Each urogomphus with 3 minute setae placed dorso-laterally. Lateral parts of abdominal segments I–VIII with single, short setae. Ventral parts of abdominal segments I–VIII without setae. Each femur without setae (Fig. 12A, B).

Discussion

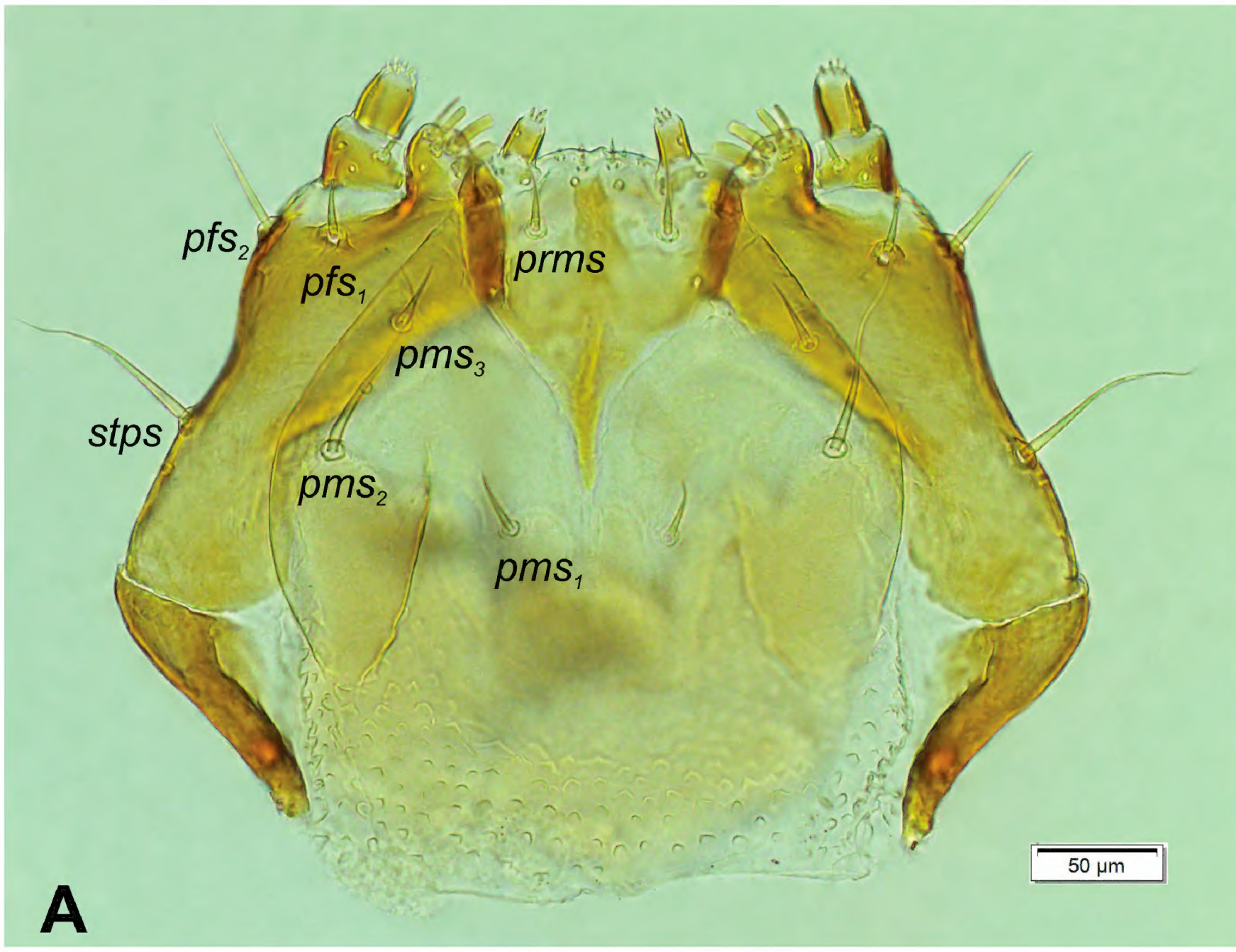
Morphology

There are several species in the genus *Anthonomus*, including *A. terreus* Gyllenhal, 1835, Curtis, 1840, *A. costipennis* Fairmaire, 1889 and especially *A. rubi*, whose morphology is very similar to that of *A. brunnipennis*. The systematic status and distribution of some of these taxa are still under debate (Legalov 2000; Alonso-Zarazaga et al. 2023).

Adults of *Anthonomus brunnipennis* are very similar to *A. rubi* and can be distinguished by differences in body size (albeit with an overlap), 1.7–2.1 mm in *A. brunnipennis*, and 2.0–3.5 mm in *A. rubi* according to Dieckmann (1968) and 1.5–2.4 mm in *A. brunnipennis*

Table 1. Morphological differences between larvae and pupae of *Anthonomus brunnipennis* and *A. rubi*.

	Anthonomus brunnipennis	***Anthonomus rubi***
larva	body yellow, strongly curved, length up to 2.66 mm	body whitish to yellowish, length up to 3.42 mm
	head brown, up to 0.56 mm in length, with 3 *pes* and 2 *ves*	head yellowish, up to 0.67 mm in length, with 4 *pes* and 0 *ves*
	thorax with 10 *prns*, 2 *prs*, 5 *pds*, 2 *ss* and 3 *pda*	thorax with 11 *prns*, 1 *prs*, 4 *pds*, 1 *as*, 3 *ss* and 5 *pda* (+2 sensillae)
	abdominal segments I–VIII with 2 *prs*, 4 *pds*, 0 *ps* and 1 *eus*	abdominal segments I-VIII with 1 *prs*, 5 *pds*, 1 *ps* and 2 *eus*
	abdominal segment IX with 3 *ds* and 0 *sts*	abdominal segment IX with 6 *ds* and 2 *sts*
	clypeus without clss	clypeus with 1 clss
	labrum with 3 *ams*,	labrum with 2 *ams*
	epipharynx with 4 snp in single cluster	epipharynx with 4 snp in two separate clusters
	labial palpi two-segmented, with 6 *dms* and 4 *vms*	labial palpi one-segmented, with 5 *dms* and 5 *vms*
pupa	body length up to 2.30 mm	body length up to 3.42 mm,
	rostrum with 1 *rs*	rostrum without *rs*,
	head with 2 *sos* and 0 *os*	head with 1 *sos*, 1 *os*
	clubs covered with conical asperities	clubs smooth
	abdominal segments I–VII with 5 *d*	abdominal segments I–VII with 3 *d*
	urogomphi fused, with separate apical parts	urogomphi paired, located close together throughout their length



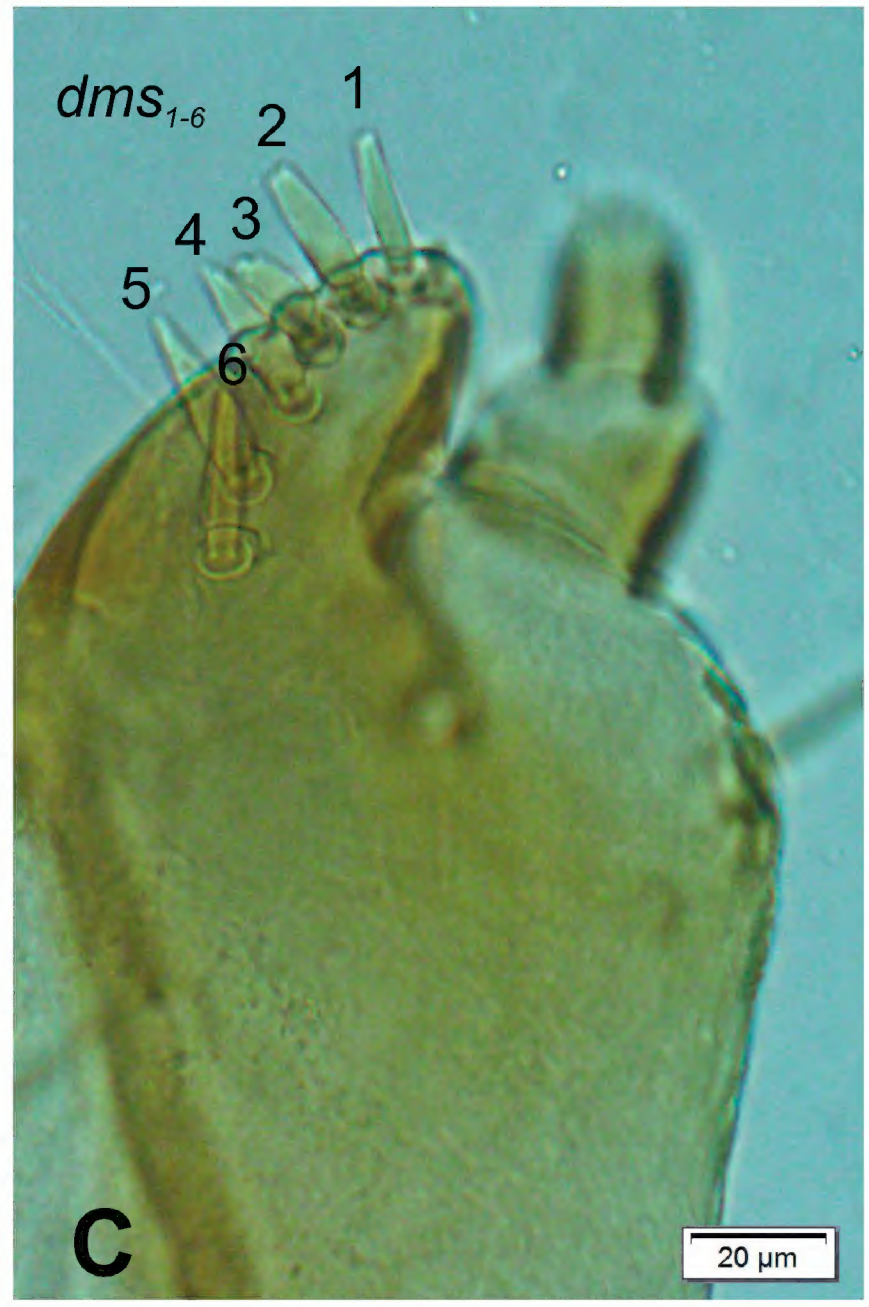


Figure 9. *Anthonomus brunnipennis* mature larva, maxillolabial complex (photos). **A.** Maxillolabial complex, ventral aspect; **B.** Apical part of right maxilla, ventral aspect; **C.** Apical part of right maxilla, dorsal aspect, (*dms*–dorsal malar, *pfs*–palpiferal, *prms*–prelabial, *pms*–postlabial, *stps*–stipal, *vms*–ventral malar, 1–6– malar setae numbers).

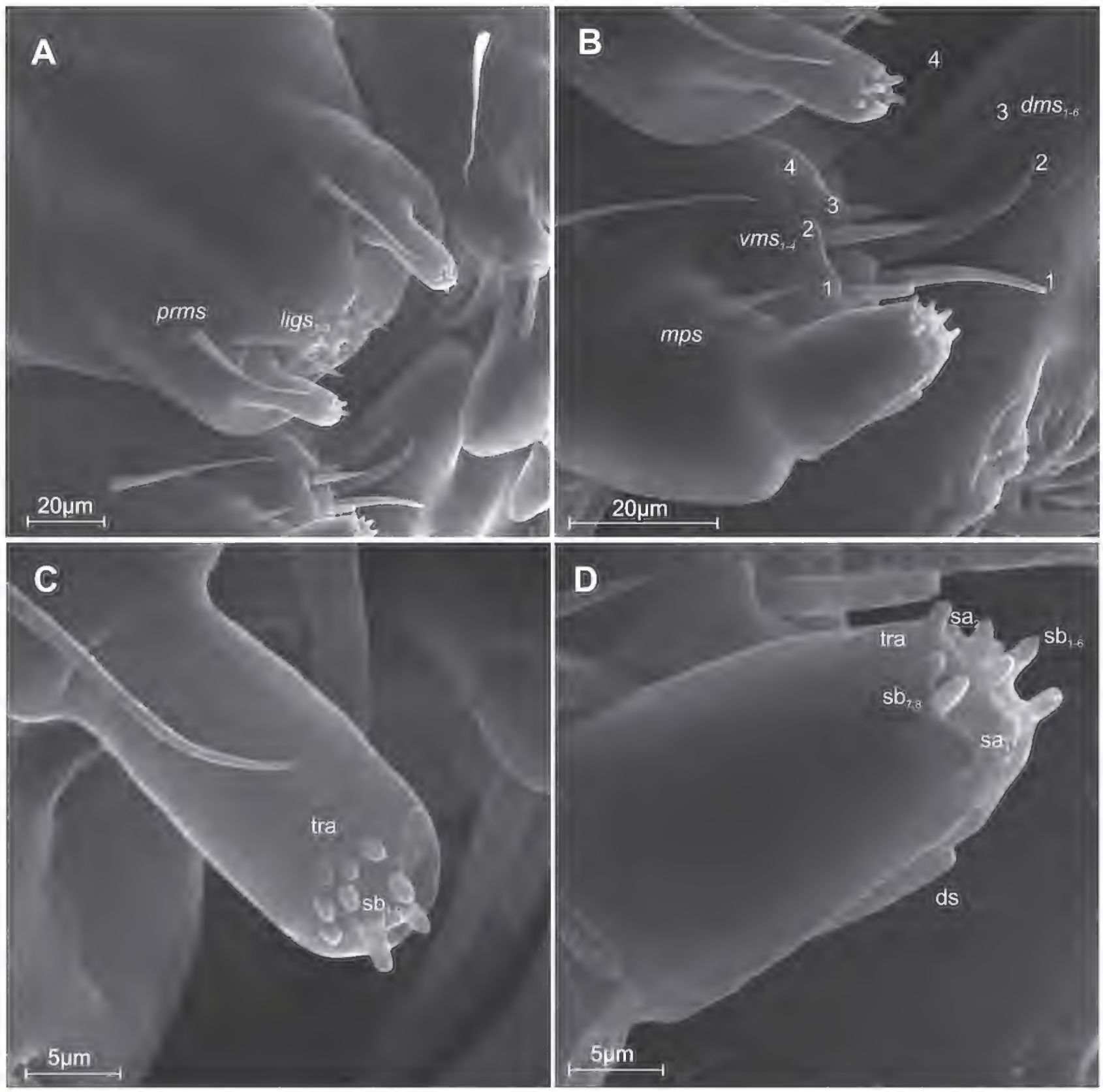


Figure 10. *Anthonomus brunnipennis* mature larva, maxillolabial complex (SEM micrographs). **A.** Prementum, ventral aspect; **B.** Apical part of right maxilla, lateral aspect; **C.** Distal, labial palpomere; **D.** Distal, maxillary palpomere (setae: *dms*–dorsal malar, *mps*–maxillary, *prms*–prelabial, *vms*–ventral malar palp; sensilla: ds–digitiform, sa–ampullaceum, sb–basiconicum; tra–terminal receptive area).

and 2.0–3.2 mm in *A. rubi* according to Palm 1992) by two separate light longitudinal fields on the aedeagus in *A. brunnipennis*, which are confluent in *A. rubi* (view from above; Palm 1992), and by the size of the aedeagus (Kevan 1965): 0.65–0.77 mm in *A. rubi* and 0.50–0.625 mm in *A. brunnipennis*. Kevan (1965) pointed out the length difference in the first antennomere of the funicle and Gurney (without date) in the second: both are more slender in *A. rubi* (Fig. 14). Other differences, e.g. body colour (Fig. 15), are not conclusive and are only of secondary importance, even if *A. brunnipennis* does tend to be dark reddish to dark brown in colour and *A. rubi* black. But immature adults may cloud this picture.

The immature stages of *A. rubi* were previously described by Scherf (1964) and Burke (1976), but the work of Zabaluev (2021) provided the most complete and detailed attempt. Thus, the immature stages of both species differ distinctly in the characters presented in Table 1.

Figure 11. *Anthonomus brunnipennis* pupa, habitus.

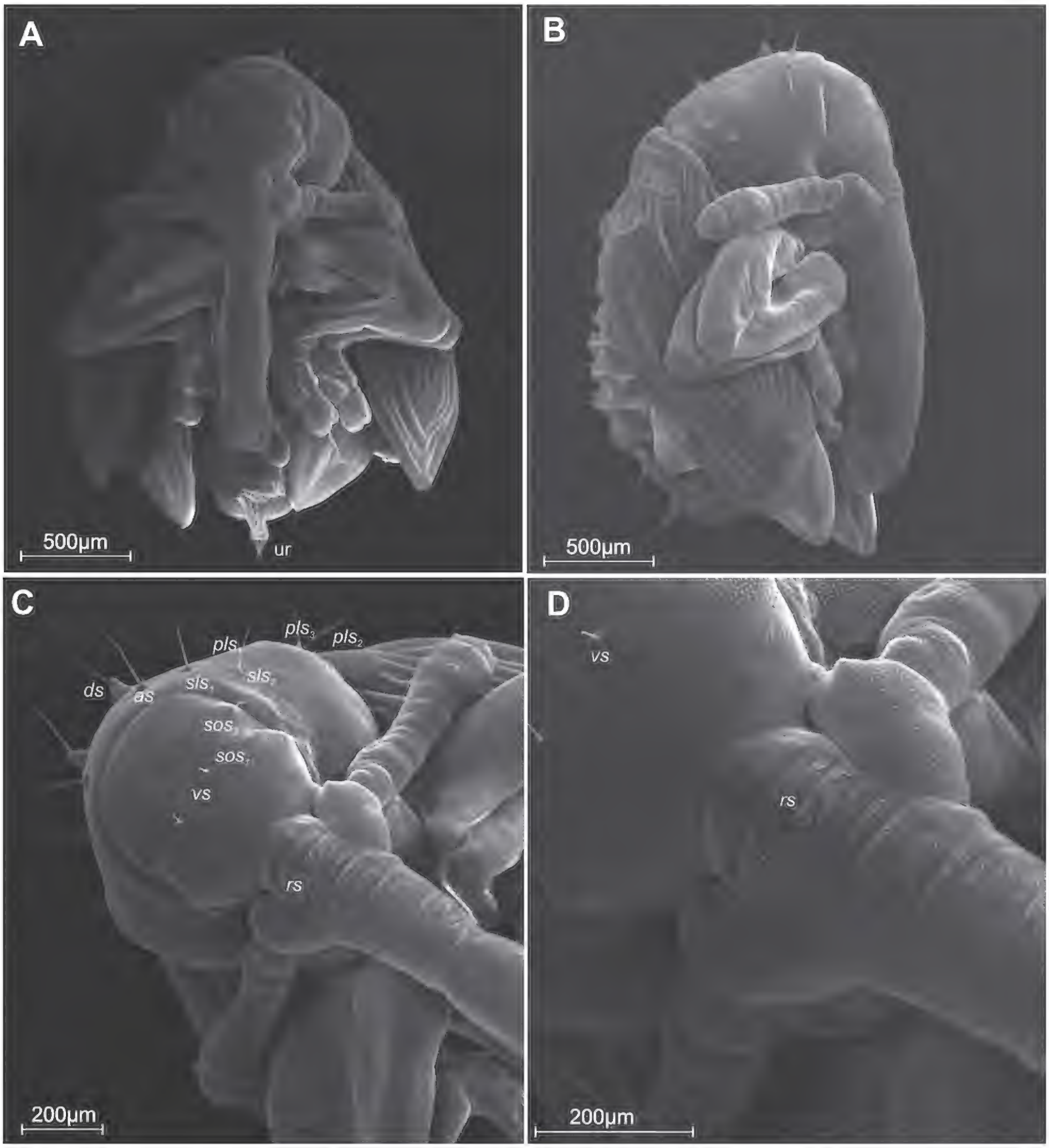


Figure 12. *Anthonomus brunnipennis* pupa (SEM micrographs). **A.** Habitus, ventral view; **B.** Habitus, lateral view; **C.** Head and rostrum base; **D.** Rostrum base magnification (ur–urogomphus, setae: *as*–apical, *ds*–discal, *sls*–lateral, *sos*–superorbital, *pls*–posterolateral, *rs*–rostral).

Based on the morphological structure of preimaginal stages, Zabaluev (2021) proposed a preliminary division of the genus *Anthonomus* into five species groups. In this division, group 3 contains *A. rubi* and *A. rubripes* Gyllenhal, 1836. Interestingly, despite the significant similarity of the adult stages, the larva of *A. brunnipennis* does not have any of the features characteristic of group 3, namely, 11 *prns* and the epipharynx with two separate clusters vs 10 *prns* and a single cluster on *A. brunnipennis*, whilst the pupa has well-defined features, prothoracic depressions and the presence of *sos*. It therefore seems that the division into species groups within the genus *Anthonomus* requires redefinition.

It should be noted that both the larva and the pupa of *A. brunnipennis* have features found almost exclusively in Nearctic species (e.g. *A. nebulosus* LeConte, *A. grandis* Boheman, *A. stupulosus* Champion, *A. flavus* LeConte, *A. texanus* Dietz and *A. albopilosus* Dietz): snp organized in a single cluster, labial palpi two-segmented; in the pupal stage: a prothoracic depression, and abdominal segments I–VIII bearing five pairs of setae, placed on protuberances; setae alternating in length with noticeably

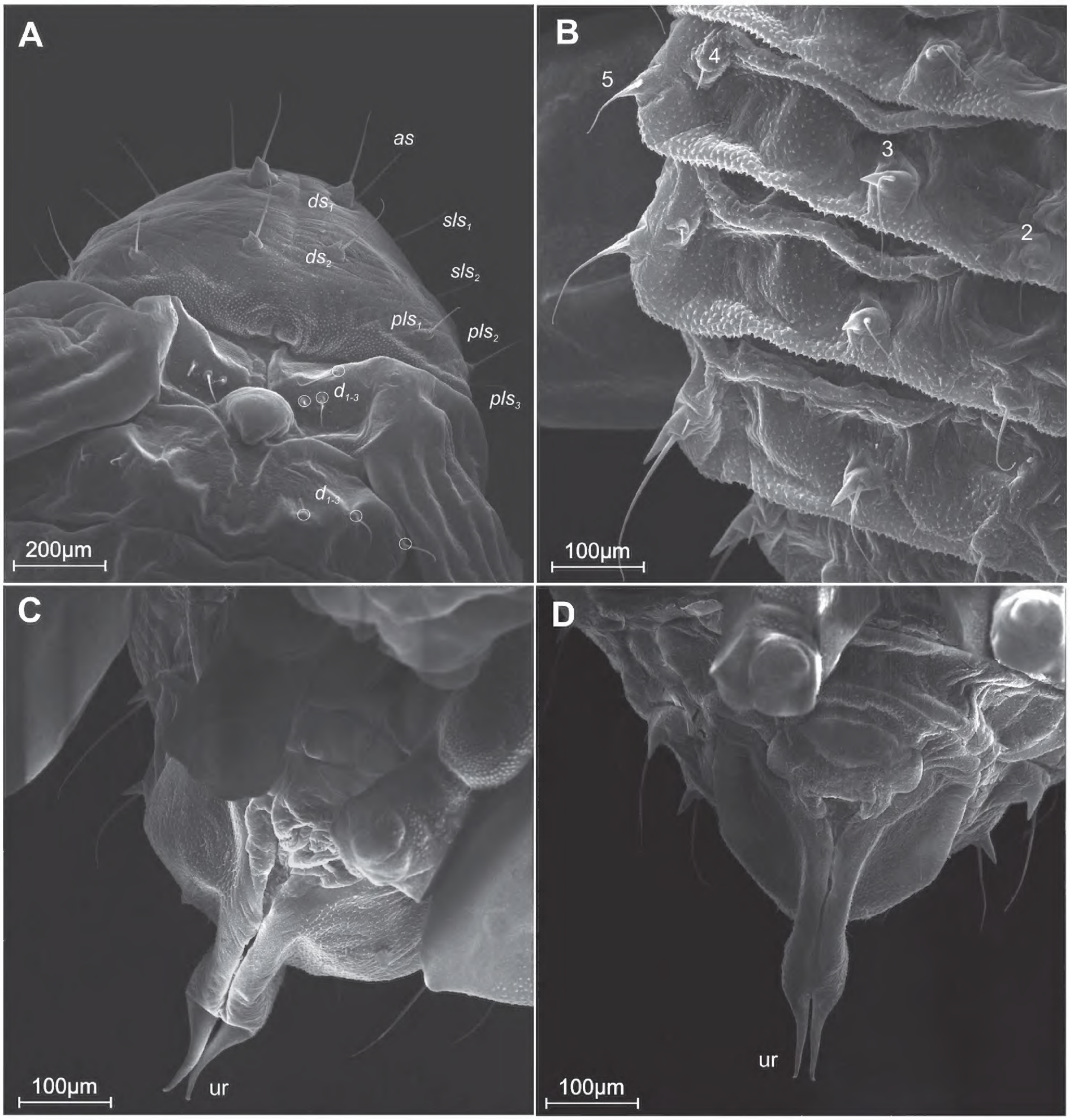


Figure 13. *Anthonomus brunnipennis* pupa, habitus and chaetotaxy. **A.** Pro–, meso– and metathorax dorsal view; **B.** Abdominal segments; **C.** Females abdominal terminal segments; **D.** Males abdominal terminal segments, magnification (ur–urogomphus, setae: *as*–apical, *d*–dorsal, *ds*–discal, *sls*–lateral, *pls*–posterolateral, 1–5– dorsal setae numbers).

shorter setae in the odd intervals. The characteristic features at the generic level of both the larva and the pupa of the genus *Anthonomus* were specified precisely by Zabaluev (2021). Hence, they do not require further elaboration. In turn, based on available descriptions (Burke 1968; Ahmad and Burke 1972; Vanin et al. 2013), the following characters are diagnostic of the genus *Anthonomus* at the larval stage and distinguish it from other genera of the tribe Anthonomini: (1) always 3 *als* (*Furcipus* Desbrochers with 2 *als*), (2) except in *A. rubi* and *A. rubripes*, snp arranged in a single median cluster of 4 units (*Smicraulax* Pierce without snp; *Anthonomopsis* Dietz, *Loncophorus* Chevrolat and *Tachypterellus* Fall & Cockerell snp arranged in two lateral clusters, (3) labral rods separate (*Pseudanthonomus* Dietz and *Coccotorus* LeConte labral rods posteriorly fused).

The pupa of *Anthonomus brunnipennis* exhibits evident sexual dimorphism in the gonotheca – divided in the female, undivided in the male – with tubercles on subcontiguous lobes. Similar structures have also been observed in the genus *Aspidapion* Schilsky, 1901 (Gosik, in press) and in *Smicronyx smreczynskii* Solari, 1952 (Sprick and Gosik 2023). According to Burke (1968) a bilobed gonotheca is a characteristic feature of female pupae.

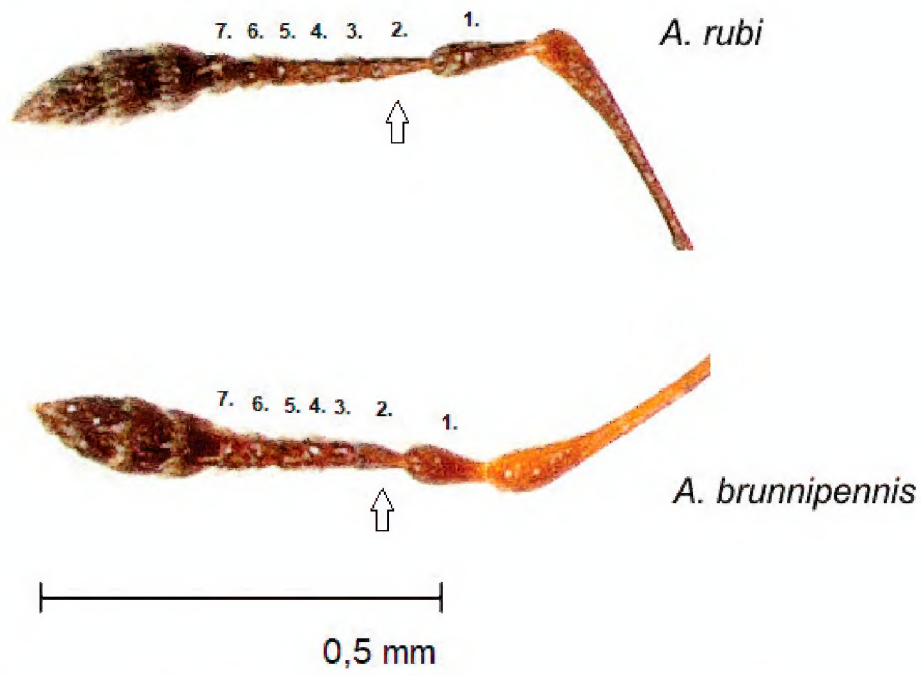


Figure 14. Comparison of antennae of *Anthonomus brunnipennis* and *A.rubi*.

Bionomics

According to literature data, *Anthonomus brunnipennis* is an oligophagous species that feeds on several plants from the family Rosaceae Juss. Dieckmann (1968), Hoffmann (1954), Koch (1992), Palm (1992) and Morris (2012) list *Comarum palustre* L. (syn. *Potentilla palustris* (L.) Scop.), *Dryas octopetala* L., *Filipendula ulmaria* and *Potentilla erecta* (L.) Raeusch. Its presence on the genus *Helianthemum* Mill. (family Cistaceae Juss.) was recorded by Tempère and Péricart (1989), even though it seems highly improbable that this genus and family are host plants of *A. brunnipennis*. Another explanation could be that weevils migrate to a plant with similar small, yellow flowers before *Potentilla erecta* starts to flower. According to Hoffmann (1954), *Filipendula ulmaria* (L.) Maxim. is also mentioned as a host plant of *A. brunnipennis*. However, the relationship between *A. brunnipennis* and this morphologically rather different species seems doubtful and requires confirmation by detailed field observations, e.g. oviposition behaviour or the presence of larvae. In Schleswig-Holstein, to date the region with the only German localities, R. Suikat found this species only on *Potentilla erecta*, even though *Comarum palustre* was growing nearby at the same locality (pers. comm. 2024) (habitat, see Fig. 2). Morris (2012) described this situation in similar words: "On *Potentilla erecta*, possibly other *Potentilla* species, and *Comarum palustre*". Dieckmann (1968) cited Crotch, who found a form of *A. brunnipennis* on *Comarum palustre* in Scotland only in very wet localities. To clarify this situation, data regarding host plants apart from *Potentilla erecta* should be confirmed by records of larvae.

On current British websites, only *Potentilla erecta* is listed as a host plant (https://www.ukbeetles.co.uk/curculioninae). Earlier data from *Comarum palustre* or some other plants, such as the widespread *Filipendula ulmaria*, have for some unknown reason not been repeated. The use of *Potentilla erecta* as a host plant in Denmark was confirmed by Palm (1992).

Figure 15. Comparison. **A.** *Anthonomus brunnipennis* male, habitus; **B.** *A. rubi* male, habitus.

It can be stated that Hoffmann (1954) lists only *Comarum palustre*, *Dryas octopetala*, and *Filipendula ulmaria* as host plants of *Anthonomus brunnipennis*, but he overlooked the main host plant, *Potentilla erecta*, what means that all his host plant data are of low reliability.

At present, only *Potentilla erecta* can be regarded as a host plant of *Anthonomus brunnipennis*, and the status of *Comarum palustre* and *Dryas octopetala* requires confirmation. The presence of *A. brunnipennis* adults in the flowers of Cistaceae, as reported by Tempère and Péricart (1989), remains doubtful. In a current barcoding study Germann et al. (2017) did not find any difference to *A. rubi* in Alpine populations collected from *Helianthemum* (Cistaceae) and from *Dryas octopetala*. At this moment Cistaceae cannot be regarded as host plant either of *A. rubi* or of *A. brunnipennis*, and Germann (2017) recommended to delete *A. brunnipennis* from the checklist of Swiss weevils.

Anthonomus brunnipennis is classified as a stenotopic, hygrophilous species and inhabits cold and usually wet, nutrient-poor sites like certain swamps, bogs, mountain and moor meadows (Koch 1992 and our own observations). Interestingly, the northern distribution of this species coincides with the previously described relationships of characters of immatures with Nearctic (northern) species. The distribution at the southern boundary of its range may be limited by warm climate conditions and may be restricted to bogs and fens, and to mountain areas, a phenomenon which is observed in other weevils, too, e.g. *Otiorhynchus*

rugifrons or *Sitona lineellus* (see Heijerman and Hodge 2005; Rheinheimer and Hassler 2010; Germann 2013).

Unlike *Anthonomus rubi*, which is a ubiquitous species, *Anthonomus brunnipennis* is a strictly stenotopic species and occurs at only a few sites with a high degree of naturalness (National Parks, reserves), especially in the southern parts of its range in middle Europe. Because these ecosystems are threatened by nitrogen entries from the atmosphere and subsequent changes to the vegetation, and also by the effects of climate warming (drought, temperature increases), *A. brunnipennis* has been identified as a highly endangered species in Germany (see Sprick et al. 2021), and may be a candidate for such a status in other countries along the southern boundary of its range.

Author Contributions

Conceptualization – R.G. and P.S.; methodology – R.G., P.S.; field research – P.S.; laboratory resources – R.G. and P.S.; data curation – R.G. and P.S.; writing—original draft preparation – R.G. and P.S.; writing—review and editing – R.G. and P.S.; visualization – R.G. and P.S.

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